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Anatomical Considerations of Pectoral Swimming in the Opah, *Lampris guttatus*

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(1936). On the other hand, the name *L. regius* has more recently been used by Fowler (1936), Smith (1965), Tortonese (1970) and Bini (1970).

As the date of publication is specified only as 1788 in the works of Bonnaterre and of Brünnich, and as there is no definite evidence to the contrary, the exact date for both publications has to be taken as 31 December 1788, in accordance with Art. 21(b) of the International Code of Zoological Nomenclature. *Lampris guttatus* and *L. regius*, therefore, are to be considered as synonyms simultaneously published, and the relative priority is determined, in accordance with Art. 24(a) of the Code, by the action of the first reviser. As first reviser, in this sense, only Müller (1806) is acceptable. He used *L. guttatus* as the name for the taxon under consideration and gave a detailed list of synonyms for the opah. Both Bonnaterre and Brünnich were cited in this list, in addition to other important works, but Müller chose to use the name *L. guttatus* in preference to any of the others. By so doing, he determined the relative priority and, in accordance with Art. 24 (a)(i) of the Code, the name *Lampris guttatus* should be used as the correct specific name for the opah.

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ANATOMICAL CONSIDERATIONS OF PECTORAL SWIMMING IN THE OPAH, *LAMPRIS GUTTATUS*.—The opah, *Lampris guttatus* (Brünnich), is a large, predatory fish of the open ocean occurring from near the surface to 500 m (Gudger, 1930). A number of papers have dealt with the anatomy and morphology of *Lampris*. The structure of the pectoral girdle has been dealt with by Boulenger (1902), Gill (1903), Jordan (1926) and Starks (1930). Le Danois (1935) described, and partially figured, the pectoral musculature, and Oelschläger (1974), in connection with his discussion on ontogenetic changes, briefly treated the pectoral anatomy, and mentioned the dark nature of the pectoral muscles, first noted by Mortimer (1750). This study was initiated when a frozen specimen (SIO74-93, 780 mm SL) was turned over to us by Al Pentiss. It was dissected, and ultimately skeletonized.

There can be little doubt that normal cruising in *L. guttatus* is accomplished by pectoral swim-

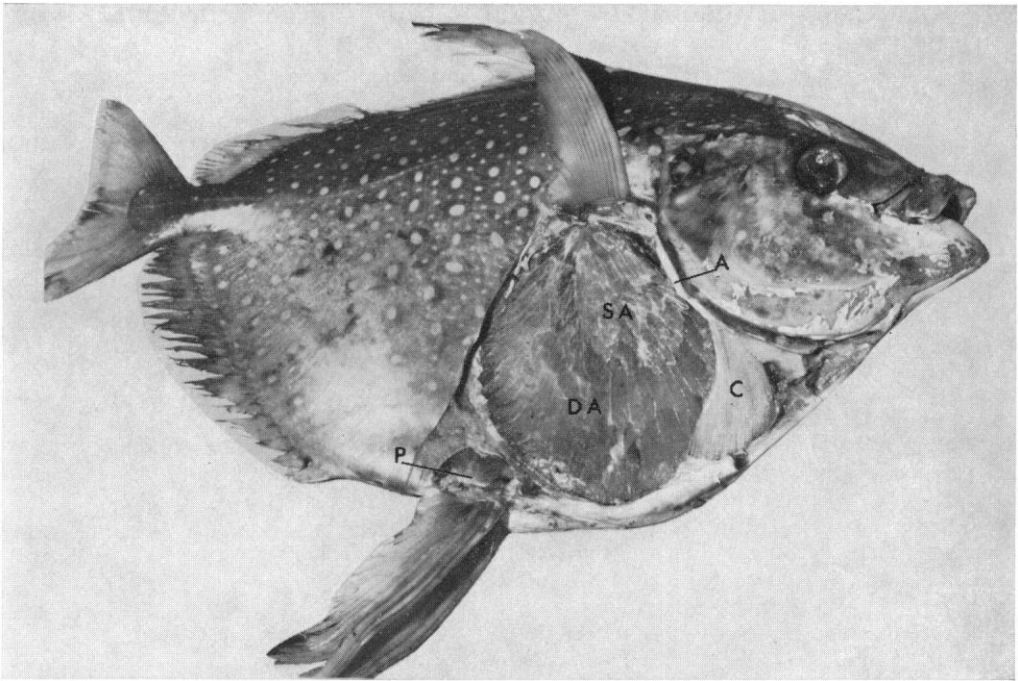


Fig. 1. *Lampris guttatus*, 780 mm SL. Oblique view of right side, pelvis and lower lobe of caudal truncated. Pectoral and pelvic musculature exposed. A, cut edge of subcutaneous adipose layer. C, exposed portion of cleithrum. DA, deep abductor. SA, superficial abductor. P, pelvic musculature.

ming. The shoulder girdle is massive and gives attachment to large, red, adductor and abductor muscles (Fig. 1). In our 28.1 kg specimen the pectoral musculature weighed 4.5 kg, or 16% of the total weight. The total lateral body musculature, determined by removing one fillet as completely as possible and doubling its weight, was 7.7 kg. (The total lateral red muscle is small, 346.8 g, making up only some 3% of the total muscle.) The pectoral muscle is thus 37% of the total propulsive musculature. This is about twice the relative amount of red muscle in the rainbow trout (Webb, 1971) and about three times the maximum value for 10 scombrid species given by Magnuson (1973). More apropos, the senõrita (*Oxyjulis californica*), a labrid which relies on the pectorals for normal locomotion and lacks lateral red muscle, has about 2% of the body weight, and 5% of the propulsive musculature as pectoral red muscle (RHR, original data). In fact the pectoral musculature of *Lampris* is probably exceeded in relative bulk only by that of the freshwater hatchet fishes (25% of body weight in *Gasteropelecus* according to Ridewood, 1913).

Microscopic examination reveals that the red

pectoral musculature of *Lampris* is rich in mitochondria and the fibers are small in diameter (G. Dobbs pers. comm.) indicating that it probably functions physiologically as red muscle. According to the currently accepted hypothesis, red muscle is aerobic and used in continuous activity, and white muscle anaerobic and used in burst swimming (Bone, 1966).

Our dissection does not agree with the multiplicity of muscles described by Le Danois. Rather, we find the normal complement (Allis, 1903; Greene and Greene, 1913; Winterbottom, 1974): a superficial abductor; an arrector ventralis; a deep abductor, divisible into an anterior and posterior part; an adductor, again with anterior and posterior divisions; and an arrector dorsalis. None of these muscles inserts on the pelvic rays, as indicated by Le Danois. The superficial adductor is much smaller than the deep one (Fig. 1), and, together with the arrectores probably serves to control the angle of attack of the pectoral fin.

An unusual feature is the presence of a thick adipose layer of lipid and connective tissue under the skin. The cut edge of this layer is visible in Fig. 1, just behind the operculum.

The adipose layer is present only over the pectoral musculature, where it is from 7.5–15 mm thick, thinning posteriorly. (Le Danois reported a "Couche de grasse" 25 mm thick in her specimen of unstated size). The lipid material is predominantly triglyceride (C. Phleger, pers. comm.).

It is tempting to speculate that the adipose layer might act as an insulator, allowing the maintenance of an elevated temperature in the pectoral musculature. However, there is no countercurrent heat-exchanger in the blood supply, making conservation of heat an apparently insuperable problem (Carey et al., 1971). Carey et al. reported a body temperature measurement for *Lampris* of only 1 C above surface ambient (depth of capture was not reported), but their measurement was almost certainly taken in the lateral body musculature. The presence of the possibly insulating adipose layer suggests that it would be of interest to determine the temperature of the pectoral red muscle in a living fish.

The bones of *Lampris* are cancellous and filled with oil, again predominantly triglyceride. For example, 73% of the dry weight of the lachrymal was oil. The oil alone is apparently not enough to confer neutral buoyancy, as there is a functional gas-bladder. Because of the presence of the gas-bladder, and uncertainty as to depth of capture, it was not possible to determine the relative buoyancy of our specimens.

Several authors have commented on the horizontal pectoral insertion of *Lampris*. Orkin (1950) cites Boulenger (1902) in stating that the pectoral cannot be raised above the midline, but the pectoral can in fact be completely appressed. The horizontal insertion of the stiff pectoral led Le Danois to hypothesize that *Lampris* must swim in a head-down attitude, in order to accelerate water backward on abduction, and thus progress. However, she did not consider that the adduction stroke would cancel any motion thus produced. In fact, the pectoral of *Lampris*, although stiff, does not have an absolutely fixed shape. There is a well developed arrector ventralis, with a strong tendon inserting on the bases of the first two rays. The superficial abductor, which in most fishes is relatively large and inserts on all the rays, here is reduced and inserts only on the posterior rays. These two muscles are well suited to control the angle of attack and camber of the fin, with the arrector inclining the anterior edge of the fin on the downstroke, and the

superficial abductor and arrector dorsalis together causing the posterior edge of the fin to trail on the upstroke. This would provide the angle of attack necessary for the generation of lift and thrust (Gray, 1968:194–197). Flapping flight of necessity generates vertical as well as horizontal propulsive forces (Webb, 1973). The large pelvic fins (1800 cm<sup>2</sup> total area) which extend out from the body, with their surfaces parallel to the direction of forward motion, could act to dampen the resultant vertical oscillation. If the angle of attack could be varied slightly, the up and down forces would be converted to thrust. Whether this actually is the case can only be determined by observations on a living individual.

Neither the pectorals nor the pelvics can be rotated normal to the direction of motion. This means that they cannot act as brakes (as surmised by Orkin, 1950) as they do in most fishes (Harris, 1953). Turning can be accomplished by using only one pectoral or, more likely, by inclining the caudal and posterior portions of the dorsal and anal to one side. We can envision no means by which sudden stops can be achieved. In the pelagic environment they may never be necessary.

Orkin (1950) felt that normal cruising in *Lampris* is achieved by caudal-swimming, and that the pectorals are used for acceleration and maneuvering. However at that time the functional significance of red and white muscle was not known. Judging from the relatively small size (1400 cm<sup>2</sup>) and high aspect ratio (6.6) of the pectorals, they should be high-speed, low-torque devices. This leads us to the following hypothesis of swimming modes in *Lampris*. Low speed swimming is the function of the caudal fin and the lateral red musculature. Acceleration to cruising speed of a few body lengths per second is achieved by burst-swimming with the lateral white muscle and caudal, with the pectorals maintaining cruising speed. Increases in fast cruising speeds are probably also achieved by burst-swimming, with the pectorals maintaining the new rate.

The fin and muscle functions hypothesized here are of necessity inferential and can only be tested by observations of swimming, and temperature measurements, of living individuals. It is hoped that this paper may stimulate such observations.

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- TUBERCULATION OF THE PEARL DACE, *SEMOTILUS MARGARITA* (PISCES: CYPRINIDAE).**—Of the three species of fish in genus *Semotilus*, the tuberculation has been described for *S. atromaculatus* (Mitchill) (Fowler, 1912; Wiley and Collette, 1970) and for *S. corporalis* (Mitchill) (Reed, 1971). However, tuberculation of *S. margarita* has been little known. Langlois (1929) reported the presence of breeding tubercles on the pectoral fins of male *S. margarita*. Recently in a life history study of this species in Hamilton Run, Maryland (Fava and Tsai, 1974), it was found that breeding tubercles are present not only on pectoral fins but also many parts of the body in both sexes. By using these specimens collected during the life history study, this paper describes the breeding tubercles of *S. margarita* and their seasonal development. A breeding male (65.6 mm standard length) and a female (68.2 mm) were selected for tubercular measurement. The mean length and diameter of the tubercles on each part of the body and fins were calculated by measuring at least five tubercles with an ocular micrometer under the dissection microscope,  $3 \times 10$  magnification.
- Tubercles on breeding males.*—Tubercles are present almost completely over the head and body. In the head region they are closely spaced in the center of the opercula and along their edges, and extend to the first and second branchiostegal rays. They are cone-shaped with an average length of 0.07 mm and 0.10 mm diameter. On the parietal, frontal and nasal areas of the head they are widely spaced and have an average length of 0.04 mm and 0.08 mm diameter. Elsewhere on the head the tubercles are more widely spaced and extremely small, length 0.02 mm and diameter 0.04 mm.
- On the body, the tubercles are present along the posterior edge of each scale. The number of the tubercles per scale varies in different regions: 1-3 on the dorsal and abdominal regions; 2-4 on the anterior portion of the chest between the pectoral fins and isthmus; 4-6 on the anterior portion of the lateral side of the body along the lateral line; and 2-10 on the caudal peduncle. The average length is 0.08 mm and diameter 0.11 mm.
- On the pectoral fins large prominent tubercles are present on the dorsal surface from the second to the eighth ray (Fig. 1). On each ray they are arranged in a single row at the base of the ray, and then split into two rows when the ray splits into two branches. The tubercles are